POPULATION DYNAMICS OF *TILLANDSIA BRACHYCAULOS* SCHLTDL. (BROMELIACEAE) IN DZIBILCHALTUN NATIONAL PARK, YUCATÁN

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ABSTRACT. Population dynamics of the epiphytic bromeliad, *Tillandsia brachycaulos,* was followed for a year (October 1996 to October 1997) in a low-statured tropical deciduous forest in the Yucatan Peninsula, Mexico. Nine hundred and twenty individuals of this species, located on nine trees of *Gymnopodium floribundum* (Polygonaceae), were tagged. The individuals were classified into two major groups according to their origin: seed or vegetative propagation. Each group was subdivided with regard to height. Bimonthly demography censuses were carried out, where growth, survival, and fecundity were reported for each individual. Results indicate that most of the individuals arise from vegetative propagation (66%), highest mortality value was found in the seedling stage (71%), highest fecundity in the adult 3 stage (2.05 seedlings/individual), whereas the highest production of offshoots is presented by the adult 3 offshoot stage (1.13 offshoots/individual). A Lefkovitch matrix model was used to estimate the population finite rate of growth (λ), that resulted in a value of 0.91.

Key words: population dynamics, Bromeliaceae, *Tillandsia brachycaulos,* matrix models, demography of *Tillandsia*

INTRODUCTION

In the last few decades, the accelerated loss of plant and animal species caused by human activities, has reached alarming numbers. It is estimated that 23% of all vascular plant species will have been lost by the end of the 20th century (Raven 1988). Some plant families such as the Orchidaceae, Bromeliaceae, Arecaceae, and Cactaceae have been threatened for some time. Therefore, one of the human priorities must be the conservation of species (Ehrlich 1988, Nadkarni 1992, Primack 1993).

Schemske et al. (1994) suggested that the recovery efforts for an endangered species require answering the following three questions: What is the biological status of the species? What are the life cycle stages that have the greatest effect on population growth and species persistence? What are the biological causes of variation in those life history stages that have a major demographic impact? Two of these questions can be answered using a demographic approach and incorporating the projection of population matrix models.

Projection matrix models can be used to explore the biological status of a population and to identify the life history stages that most affect the population finite rate of increase (λ) (Caswell 1989, van Groenendael et al. 1988). Transition matrices are used to estimate λ while elasticity matrices are used to measure the change in the value of λ in response to relative changes in the value of a matrix element (de Kroon et al. 1986, Caswell 1989).

Some population dynamics studies that use projection matrix models attempt to estimate the regenerative capacity of the species and determine which are the most vulnerable stages of the life cycle, with the objective of applying this information to conservation and management plans for several species (Peters 1991, Pinard & Putz 1992, Durán & Franco 1995, Martinez & Alvarez-Buylla 1995, Olmsted & Alvarez-Buylla 1995).

Unfortunately, there are few studies of population dynamics of epiphyte species (Benzing 1981, Larson 1992, Hietz 1997), and even fewer that use the projection matrix models (Tremblay 1997, Hernández-Apolinar 1992). Epiphytes are organisms that spend a major portion of their life cycle situated on other plants without taking nutrients directly from the host plant (Benzing 1990). They play an important role in tropical ecosystems where they contribute significantly to the richness and abundance of species (Gentry & Dodson 1987).

Habitat destruction and illegal exploitation have threatened many populations of epiphyte species (Hernández-Apolinar 1992, Larson 1992, Rauh 1992). In consideration of this situation, the generation of information that helps to understand the behavior of the populations of epiphytic species is of crucial importance.

Among vascular plants, Orchidaceae, Araceae, and Bromeliaceae contain the highest percentage of epiphytic species (Kress 1986). In the Bromeliaceae, the neotropical genus *Tillandsia*

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comprises the largest number of epiphyte species. Unfortunately, many species of *Tillandsia* have become fashionable ornamental plants on the European and Japanese markets (Rauh 1992), which has occasioned the illegal collection of many species. Seven species of *Tillandsia* are listed in CITES as endangered and 14 more species have been suggested by Rauh (1992) to be included.

The purpose of this study is to analyze the population dynamics of *Tillandsia brachycaulos,* determine the status of populations in Dzibilchaltun National Park, and learn which are the most vulnerable stages of the life cycle.

MATERIALS AND METHODS

Fieldwork took place from October 1996 to October 1997 in a low-statured dry tropical forest in the National Park of Dzibilchaltún in the state of Yucatán in Mexico (21°05'N, 89°93'W). According to García (1964), the study site is in an area with a subhumid climate, with a dry season usually lasting from December to May. Average annual precipitation is 879 mm, average annual temperature is 25.8°C (Thien et al. 1982). The vegetation is deciduous, with a maximum canopy height of 8 m. *Bursera simaruba* (Burseraceae), *Caesalpinia gaumeri* (Caesalpiniaceae), *Piscidia piscipula* (Fabaceae), and *Gymnopodium floribundum* (Polygonaceae) are common tree species. The epiphytic community is formed by species of Cactaceae, Orchidaceae, and Bromeliaceae, the latter being one of the most diverse families in the area. Within the Bromeliaceae, the genus *Tillandsia* is represented with the most species: *T. paucifolia, T. recurvata, T. schiedeana, T. elongata* var. *imbricata, T. fasciculata,* and *T. brachycaulos,* the latter being the most abundant at the study area (pers. obs.).

Tillandsia brachycaulos is an epiphytic species, native to Southern Mexico, and Central America to Panama. The plant is a stemless monocarpic rosette with numerous subrosulate 12–26 cm long leaves, the laminae densely and finely lepidote. All leaves turn an attractive reddish crimson color at flowering time, and from the center of the rosette emerge a dozen erect flowers with linear, lilac-colored, tubular petals 5–7 cm long; the stamens and pistil are exerted; the capsule is cylindrical, acute, 4 cm long. After flowering, the rosette dies and produces 1 or 2 offshoots (pups) in the axil of basal leaves (Utley 1994). In Dzibilchaltun, *T. brachycaulos* is found growing on phorophytes such as *Phyllostylon brasiliense* (Ulmaceae), and *Acacia gaumeri* and *Pithecellobium dulce* (Mimosa-

TABLE 1. Categories (life cycle stage) and their size ranges in *Tillandsia brachycaulos* populations in Dzibilchaltun National Park based on rosette height.

Category	Height range (cm)
Seedling (s)	>0.4
Infantile (i)	0.5–2.4
Juvenile (j)	2.5–4.9
Adult 1 (a1)	5–7.9
Adult 2 (a2)	8–11.4
Adult 3 (a3)	>11.5
Infantile offshoot (io)	0.5–2.4
Juvenile offshoot (jo)	2.5–4.9
Adult 1 offshoot (ao1)	5–7.9
Adult 2 offshoot (ao2)	8–11.4
Adult 3 offshoot (ao3) plants	>11.5

ceae), but is most commonly found on *Gymnopodium floribundum.*

In order to understand the population dynamics of *Tillandsia brachycaulos* in the park, fecundity, survival, and growth of all accessible individuals of this species, located on nine trees of *Gymnopodium floribundum* (in three plots randomly selected to cover spatial variability), were followed for a period of a year. Each individual was tagged with a number. The individuals were classified into two major groups according to their origin, i.e., individuals arising from seeds or individuals arising by vegetative propagation. Each group was subdivided into height categories (measured from the base of the rosette to the top of it). Each category within each group represents individuals with similar growth rates, survival, fecundity, and vegetative propagation. In order to compare between groups, analogous stages were created within each one, except for the seedling stage. Thus, plants were placed in one of the eleven stages (TABLE 1) and the population structure was determined.

A census of all tagged individuals was carried out every two months where height, rosette architecture, survival, number of capsules, and offshoots produced by each individual were scored.

With the information of the census, the fate of each individual after a year was determined. The individuals may have different fates. They may transit from one stage to another, stay in the same stage, die, or produce seeds and/or offshoots. With these data, the different probabilities for the population were performed: transition (g) was calculated as the proportion of individuals of each stage that moved to another stage; stasis (s) was estimated as the proportion of individuals that stayed alive in the same
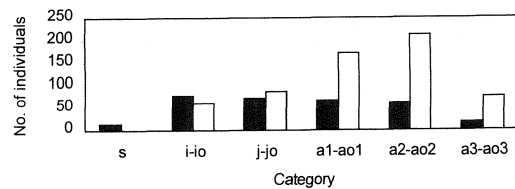
FIGURE 1.   Population structure in the October 1996 census. In each category the first column represents the individuals originated from seed, the second column represents individuals originated from vegetative propagation. Categories as in TABLE 1.
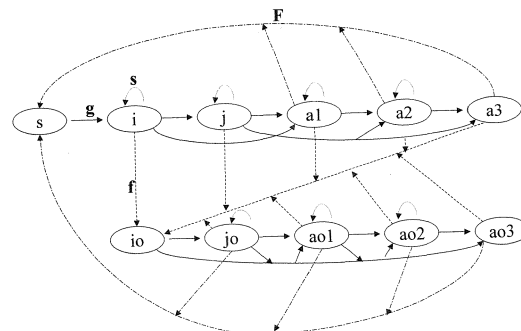

FIGURE 2.   Life-cycle diagram of *Tillandsia brachycaulos*. Only adult individuals introduce new individuals to the population, through seed and/or vegetative propagation: **g** (solid line) indicates the probabilities of moving from one stage to another; **s** (dotted line) represents the probabilities of staying in the same stage; **F** (long dash/dotted line), the number of seedlings for each individual sampled stage; **f** (dashed line) represents the number of offshoots for individuals on each sampled stage. Categories as in TABLE 1. See text for details.

stage. The fecundity (F) was calculated on the basis of the average number of seeds/individual per stage, multiplied by 0.25. Based on field observations, this value was arbitrarily assigned, and represents a very optimistic estimation with regard to the dispersal of seeds to a safe site (to have a better estimate of this probability, a seed dispersal experiment is being carried out). The resulting number was multiplied by 0.024. This value represents the percentage of germination obtained in a field experiment. Vegetative propagation per stage (f) was estimated as the number of offshoots per individual.

Using field data, a life-cycle diagram was created and the values of the demographic processes (growth, stasis, fecundity, and propagation) were used to make a Lefkovitch matrix model to estimate the finite growth rate of the population (λ).

RESULTS

The original population structure, established in October 1996 using the categories shown in TABLE 1, is represented in FIGURE 1. Most of the individuals originated from vegetative propagation (66%), and 34% of the individuals originated from seed. Considering both groups, the intermediate stages (juvenile, adult 1, adult 2) are the most abundant. The latter three categories, resulting from vegetative propagation alone, compared to the total number of individuals of the population (920) made up 51% of the individuals. Twenty-three percent of the individuals originated from seed. Infantile stages were well represented (6.6% and 8.4%) as well. The

least represented is the seedling stage (0.15%) followed by adult 3 stage (1.9%).

The estimated values for mortality, fecundity, and propagation are displayed in TABLE 2. Based on the monocarpic nature of the rosettes, the highest value of mortality corresponds to categories adult 2, adult 3, adult 2 offshoot, and adult 3 offshoot. Among the non-adult stages, the highest mortality is found in the seedling stage (71%), where most of them die when they fall off the phorophyte.

The highest values of fecundity and vegetative propagation are presented in the largest stages (a2, a3, ao2, ao3). Even though the production of offshoots normally occurs after the individual has flowered, it may also occur when individuals die without flowering, even in the infantile stage.

The life cycle diagram of *Tillandsia brachycaulos* is shown in FIGURE 2. It is a complex diagram which indicates the fate of individuals originating from two different forms of regeneration, vegetative propagation, and reproduction by seeds. The diagram shows the possible transitions that may occur with the individuals

TABLE 2.   Values of mortality (% M), fecundity (F, as no. of seedlings/individual), and vegetative propagation (P) (No. offshoots/individual), as occured from October 1996 to October 1997. Categories as in TABLE 1.

Stages	s	i	j	a1	a2	a3	io	jo	ao1	ao2	ao3
M	71	40	34	69	85	100	52	43	60	88	100
F	0	0	0	0.394	0.941	2.02	0	0.05	0.596	1.369	1.966
P	0	0.039	0.108	0.448	0.754	0.94	0.246	0.3	0.462	0.897	1.131

TABLE 3. Projection matrix corresponding to the life cycle diagram of *Tillandsia brachycaulos*. Categories as in TABLE 1; *N* represents the number of individuals per category found in October of 1996.

	s	i	j	a1	a2	a3	io	jo	ao1	ao2	ao3
s	0	0	0	0.394	0.941	2.05	0	0.052	0.596	1.369	1.96
i	0.286	0.167	0	0	0	0	0	0	0	0	0
j	0	0.33	0.189	0	0	0	0	0	0	0	0
a1	0	0.103	0.378	0.134	0	0	0	0	0	0	0
a2	0	0	0.081	0.179	0.066	0	0	0	0	0	0
a3	0	0	0.014	0	0.082	0	0	0	0	0	0
io	0	0.039	0.108	0.448	0.754	0.94	0.246	0.3	0.462	0.897	1.13
jo	0	0	0	0	0	0	0.033	0.57	0	0	0
ao1	0	0	0	0	0	0	0.148	0.183	0.035	0	0
ao2	0	0	0	0	0	0	0.18	0.207	0.193	0.037	0
ao3	0	0	0	0	0	0	0.115	0.126	0.175	0.066	0
N	14	78	74	67	61	18	61	87	171	213	76

of *Tillandsia brachycaulos* during one year. Along the solid arrows (g) an individual may advance more than one category, especially individuals originated from vegetative propagation, or may stay in the same category (s). At the same time, one may observe that an adult individual may incorporate new individuals either as seedling (F) or as offshoot (f).

The analysis of the transition matrix (TABLE 3) resulted in a finite growth rate (λ) of 0.91. The stable distribution (w) (FIGURE 3), that represents the proportional distribution of individuals of each stage when the value of λ is stable, shows that the population of *Tillandsia brachycaulos* will be made up mostly of seedling (30%) and infantile offshoot (29%) stages. The high number of seedlings calculated with the stable population structure (w) was strongly influenced by the probability of dispersion (0.25) used in the calculation of the fecundities. If the probability of dispersion factor were to be reduced, the stable population structure (w) would change. The proportion of the individuals of the rest of the stages is more or less similar for individuals originated from vegetative propagation and for individuals originated by seeds.

The reproductive value at stable distribution (v) measures the value of an individual as a seed for future population growth, and represents the amount of future reproduction, the probability of surviving to realize it, and the time required for the offspring to be produced (Caswell 1989). As is shown in FIGURE 4, the highest reproductive values for the population of *Tillandsia brachycaulos* are in the oldest categories, in both types of individuals.

DISCUSSION

This study presents the preliminary results of the first study of the population dynamics of a species of *Tillandsia* using matrix models. *Tillandsia brachycaulos*, even though it is not considered to be endangered, is a commercial species and usually abundant, the latter being the reason why it is extracted from natural populations.

This study shows some interesting results.To begin with, the original population structure displays two patterns: one for individuals originating from seed having a descending pattern, i.e., the largest numbers of individuals are in the
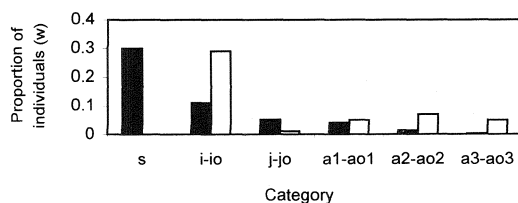

FIGURE 3. Stable structure of the population (w). The first column represents the proportion of individuals of the population originating from seed, the second column represents the proportion of individuals of the population originating from vegetative propagation. Categories as in TABLE 1.
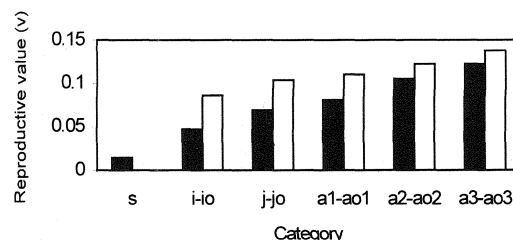

FIGURE 4. Reproductive value (v). The first column represents individuals originating from seed, the second column represents individuals originating from vegetative propagation. Categories as in TABLE 1.

younger categories (except seedlings). The other pattern, i.e., of individuals arising from vegetative propagation, presents the majority of the individuals in the intermediate categories. This suggests that the selection pressures on the individuals of the two origins of these populations are very different.

The population structure encountered in October of 1996 is very different from the stable stage structure predicted by the analysis. This suggests that the population is far from being in equilibrium. The latter may be due to the fact that the rate of growth, fecundity and mortality observed were different from those of earlier years, probably due to the arbitrary factor of dispersion (0.25) used in the analysis, or that perturbations occurred which changed the population (Mendoza 1994, Martínez & Alvarez-Buylla 1995).

Another important aspect is that vegetative propagation plays an important role in maintaining the population of *Tillandsia brachycaulos.* The high proportion of individuals originating from vegetative propagation sustains this statement. Contrary to data reported for other species with vegetative propagation (Lovett 1981, Augspurger 1985, Mendoza 1994, García-Franco & Rico-Gray 1995), the recruitment of new individuals originating from seed in *T. brachycaulos* is low, but frequent. These findings agree with Benzing's (1981) suggestion that epiphytic plants require an extraordinary combination of vegetative propagation (to secure colonized sites) and the production of vagile seeds to conquer new sites.

The few seedlings found, and their high mortality, suggest that the bottleneck of *Tillandsia brachycaulos* populations is the establishment and survival of the seedlings, as in many other epiphytic species. Benzing (1978), in a germination experiment of *Tillandsia circinnata* (Bromeliaceae), found that although germination in the laboratory was high, in the field it only reached 3.04%, and the seedlings had low survival in the field (Benzing 1981). Hernández-Apolinar (1992) reported similar results with germination of 100% in laboratory and only 3.5 $\times$ 10^{-5}% in the field for *Laelia speciosa* (Orchidaceae), while Larson (1992) reports low seedling survivorship (15.5%) for *Encyclia tampensis* (Orchidaceae). Ackerman and Zimmerman (1996) report the same tendency for *Tolumnia variegata* (Orchidaceae).

The finite population growth rate (λ = 0.91) indicates that the population is decreasing. Given the abundance of individuals of *Tillandsia brachycaulos* which is observed in the Park, one would expect that the population should be increasing or at least be at a stable stage. The rea-

son that the value of lambda is less than 1 could be due to the fact that the mortality rates were very high (0.67), which may be the result of the fact that the majority of the individuals (66%) were found in the reproductive stages (a1, a2, a3, ao1, ao2, and ao3). Given the monocarpic nature of the rosettes, they die shortly after fruiting. The high percentage of fallen individuals (11.3%) this year may also be responsible.

The preliminary results of this study help us in answering two of the questions made by Schemske et al. (1994), for the implementation of management plans and conservation of a species. We can say that the population of *Tillandsia brachycaulos* in the National Park of Dzibilchaltun is decreasing slightly (estimated value λ = 0.91), and it seems that the seedlings are the most vulnerable stage of the life cycle, based on the observed mortality of this category. This information has to be considered carefully as demographic parameters (growth, survival, and fecundity) may change over time and space (Caswell 1989, Durán & Franco 1995).

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